

澜沧蕘花(瑞香科)的花部形态发生 及其系统学意义

齐耀东 王印政*

(中国科学院植物研究所 北京 100093)

Floral morphogenesis of *Wikstroemia delavayi* (Thymelaeaceae) and its phylogenetic implication

QI Yao-Dong WANG Yin-Zheng*

(Institute of Botany, the Chinese Academy of Sciences, Beijing 100093)

Abstract Floral morphogenesis of *Wikstroemia delavayi* Lecomte was investigated by scanning electron microscope (SEM) and compared with its allied groups. Initiation and early development of floral parts in *W. delavayi* followed unidirectional sequences from the abaxial side to the adaxial side. Because the floral parts grew faster at the adaxial side than at the abaxial one in following development, the zygomorphic pattern in the early development changed and finally became an almost actinomorphic form at anthesis. The disc was initiated from the abaxial base of the floral tube and its lobes were alternate with lower whorl stamens. According to this initial and developmental pattern, it is reasonable to interpret the disc as a part of the androecium rather than a modification of the receptacle. The located position and development of the disc was correlative with the development of other floral organs, which might provide insight to delimit *Wikstroemia* and *Daphne* based on different floral developmental pattern that might exist between the two genera. The developmental process of *W. delavayi* indicated that the syncarpous and uniloculate gynoecium was in fact bicarpellate, which consisted of a fertile carpel and a sterile one. It was pseudomonomerous. Even though the ovary in both *Wikstroemia* and *Daphne* was uniloculate, the location of the ventral bundles in the ovary was obviously different from each other according to data to date. In this respect, further investigation is undertaken between the two genera.

Key words Floral morphogenesis; Zygomorphy; Disc; Pseudomonomerous gynoecium; *Wikstroemia delavayi*; Thymelaeaceae

The genus *Wikstroemia* is traditionally considered as closely related to *Daphne* (Hamaya, 1955, 1959; Hou, 1960; Tan, 1980; Dute *et al.*, 1996). In earlier systems, the delimitation of the two genera is based mainly on the shape of the disc, which is scale-like in *Wikstroemia* and annular or cup-shaped in *Daphne* (Bentham & Hooker, 1880; Gilg, 1894). However, as more and more new species have been described, the two genera become unclearly separable because of frequently transitional forms of the shape of the disc. In addition, it is debatable whether the shape of the disc should be taken as a main criterion for the delimitation of the two genera or not (Hamaya, 1959, 1963; Tan, 1980). Donke (1932) transferred some species originally placed in *Daphne* and related genera into *Wikstroemia*, for they were characteristic of the scale-shaped disc. Meisner

(1857) divided *Wikstroemia* into two sections: *Euwikstroemia* and *Diplomorpha*. Nakai (1928) lifted sect. *Diplomorpha* to generic level. Disagreeing with those who recognized the shape of the disc as an important diagnostic feature, Hamaya (1959) supported Nakai's treatment based on the evidence from anatomy of vegetative organs. He further indicated that *Wikstroemia sensu stricto* (excluding sect. *Diplomorpha* Meisner) was closer to the ancestral group than *Daphne* and *Diplomorpha*. Considering the fact of the transitional forms in the shape of the disc and other morphological characters, Halda (1999) combined *Wikstroemia* and *Daphne* into one genus *Daphne* in his recent treatment. As for the nature of the hypogynous disc in the thymelaeaceous flower, it has also been a question at issue whether the disc is a modification of the receptacle (Gerber, 1899) or a part of the androecium (Heining, 1951) or an independent glandular structure of entomophilous flowers (Skottsberg, 1972).

It is usually suggested that gynoecia of most thymelaeaceous flowers are formed by a single carpel. Especially, the gynoecia of *Daphne* and *Wikstroemia* are, in any case, considered as comprising a single carpel (Gilg, 1894; Johnson, 1931; Lawrence, 1951). However, Heining (1951) considered that the completely syncarpous gynoecium was composed of two carpels on the basis of the carpellary vascular data of 11 genera in this family. But the genus *Wikstroemia* wasn't included in Heining's study. In the revision of the Hawaiian *Wikstroemia* Skottsberg (1972) noted that the bicarpellary origin of the gynoecium in *Wikstroemia* was clearly indicated by a series of structural variation of the stigma. This indication in mature structure needs to be further confirmed by intensively developmental study with representative species in *Wikstroemia*.

In addition, the flowers in the Thymelaeaceae are usually considered as actinomorphic or regular (Bentham & Hooker, 1880; Gilg, 1894; Hutchinson, 1967). However, Hamaya (1959) described their floral aestivation as "lobes 4, outer 2 larger than the others, imbricate". Similar description of the flower of *Daphne* and *Wikstroemia* is frequently met in *Flora of Malaysia* (Hou, 1960) and *Flora Reipublicae Popularis Sinicae* (Huang & Zhang, 1999). According to them, the floral symmetry of the two genera should be bisymmetric. Furthermore, an observation in the field showed that the floral tube slightly bent to the inflorescence axis, and the floral lobes are different in size between the abaxial-to-adaxial (outer) ones and the lateral (inner) ones in *Wikstroemia*.

All above issues in the Thymelaeaceae, especially *Wikstroemia* and *Daphne*, are debated on the morphology and variation of the mature structure of the floral organs. However, it is difficult to trace the homology of the mature structure without the evidence from developmental analysis. Developmental data often offer insights into the origin of a particular structure and the evolutionary relationship that may exist in related taxa (Crisci & Stuessy, 1980). Therefore, selecting the species *W. delavayi* as the representative of *Wikstroemia*, our research mainly aimed at exploring the developmental basis for the differentiation and arrangement patterns of the floral organ in *Wikstroemia*, and revealing the origin and homology of some important floral structures in *Wikstroemia* and related taxa. The phylogenetic relationship between *Daphne* and *Wikstroemia* had been discussed on the basis of the available data.

1 Materials and Methods

Materials of *W. delavayi* Lecomte were collected in August 1999 from Yulong (Jade-dragon) Snow Mountain, Yunnan Province. Flowers of all developmental stages were fixed in formalin-acetic acid-alcohol (FAA, formalin:acetic acid:70% ethanol = 1:1:18). Voucher specimens (Qi Yao-dong No.25) were deposited in the China National Herbarium (PE). Materials were generally examined and dissected in 95% ethanol, and dehydrated in an ethanol/amyacetate series, and critical

point dried with Hitachi HCP-2 Dryer. Samples were then mounted on a stubs and Au/Pt sputter coated with SPI-Module Sputter Coater. Prepared samples were examined with Hitachi S-800 Scanning Electron Microscope (SEM) and recorded on Shanghai Panchromatic film.

2 Result

The paniculate inflorescence was terminal (Fig. 37: 1). The pedicel was articulated (Fig. 10). The floral tube was cylindric, and slightly bent to the adaxial side (Fig. 37: 2); Four floral lobes were imbricate with the abaxial and adaxial lobes overlapping two lateral lobes, in which the abaxial lobe was outmost. The two abaxial-to-adaxial lobes were slightly longer than the two lateral lobes at anthesis (Fig. 10, Fig. 37: 2). Long scale-like hypogynous disc was located at the abaxial side between ovary and lower whorl stamens adnated to the floral tube.

2.1 Floral initiation and development

The inflorescence apex successively detached floral primordia in a helical acropetal sequence, anticlockwise (Fig. 1) or clockwise (Fig. 2). The primary floral primordium was obliquely cone-shaped with a gradual slope from the narrow adaxial bottom to the wide abaxial top (Figs. 1, 2). As enlarged, the floral primordium gradually became ellipsoidal (Figs. 2, 3). It further flattened when floral lobes were initiated (Figs. 3, 4).

The abaxial floral lobe appeared first (Fig. 4), followed by the adaxial floral lobe and two lateral floral lobes, in which the adaxial one arose slightly earlier than the two lateral ones (Fig. 5). As floral lobes grew upward, the lateral growth at their bases connected the four floral lobes into a floral tube (Figs. 6, 7). The adaxial lobe first overlapped the two lateral lobes (Figs. 8, 9), then the outmost abaxial lobe covered the three ones (Fig. 10). This imbricate aestivation in bud was characteristic of a decussate pattern of floral lobes, outer with the adaxial to abaxial pair and inner with the lateral pair (Figs. 9, 10). As the floral lobes were getting closed, the floral tube grew rapidly and bent slightly to the adaxial side (Figs. 9, 10). At anthesis, the floral tube was three quarters of the flowers in length, and the abaxial and adaxial lobes were almost equal in size (Fig. 37: 2).

2.2 Stamen initiation and development

Following the closure of the floral lobes, the upper whorl stamen primordia appeared at the base of the floral tube. The abaxial stamen was initiated first, followed by two lateral ones simultaneously; the adaxial stamen arose last (Fig. 11). Accompanying the enlargement of the upper whorl stamens, the lower whorl stamens appeared in the sequence from the two abaxial stamens to two adaxial ones (Fig. 12).

As the upper whorl stamens with different size differentiated into filament and anther, the lower whorl stamens became almost equal in size (Fig. 13). When the pistil was about 144 μm in height, in the upper stamens the median furrow and the transverse furrow could be seen in the abaxial and lateral stamens (Fig. 20), whereas only the median furrow became visible in the smaller adaxial one (Figs. 18, 20). At this stage, the lower whorl stamens were smaller than the upper whorl ones (Figs. 13, 18, 20). When the disc was initiated, the abaxial stamen was still larger than the others in the upper whorl (Fig. 27). The adaxial stamen remained somewhat smaller than the other three in the upper whorl until the disc was about 6 μm in height (Fig. 31). During development the lower whorl stamens were always smaller than the upper whorl ones, but difference in size between two whorls was diminished gradually (Figs. 27, 31). At anthesis, all stamens in two whorls were equal in size (Fig. 36).

2.3 Gynoecium initiation and development

While stamens arose sequentially, the remained floral apex became dome-shaped in the center of the flower (Figs. 11, 12). The floral apex flattened to a tetragonal form as lower whorl stamens primordia enlarged and leaned against it (Figs. 13, 14). The two carpellary primordia arose as the adaxial and abaxial regions were elevated from the tetragonal floral apex (Fig. 15). In each carpellary primordium, a slope was formed from the dorsal summit to the lower ventral region because of more rapid growth at the dorsal side (Fig. 16). At inception the abaxial carpel was slightly higher than the adaxial one (Figs. 15, 16). As grew upward, two carpels fused gradually at the lower ventral regions (Fig. 17). Because of more active growth of the adaxial carpel, it soon exceeded the abaxial carpel in height, and infolded toward the abaxial side. (Figs. 17, 19; Figs. 20 ~ 22). As stigma formed, the adaxial carpel occupied almost the whole region of the gynoecium, while the abaxial carpel only remained at the mid-abaxial point from top view (Figs. 21 ~ 24). Meanwhile, hairs appeared and developed on the surface of the ovary (Figs. 21 ~ 24), and papilla arose on the surface of the stigma (Figs. 24, 25). Two integuments became visible in the solitary ovule that was borne on the abaxial sub-top of the ovarian wall (Figs. 25, 26). In the mature ovary, four carpellary bundles were found in the ovarian wall at the level where the ovule was borne. In the four carpellary bundles, two dorsal bundles were located at the median position of the adaxial and abaxial sides respectively, while two ventral bundles were in the lateral position near the dorsal bundles at the abaxial side (Fig. 26). Finally, a bottle-shaped pistil was formed with hairs on the surface of the ovary and papillate hairs on the surface of the stigma (Fig. 35).

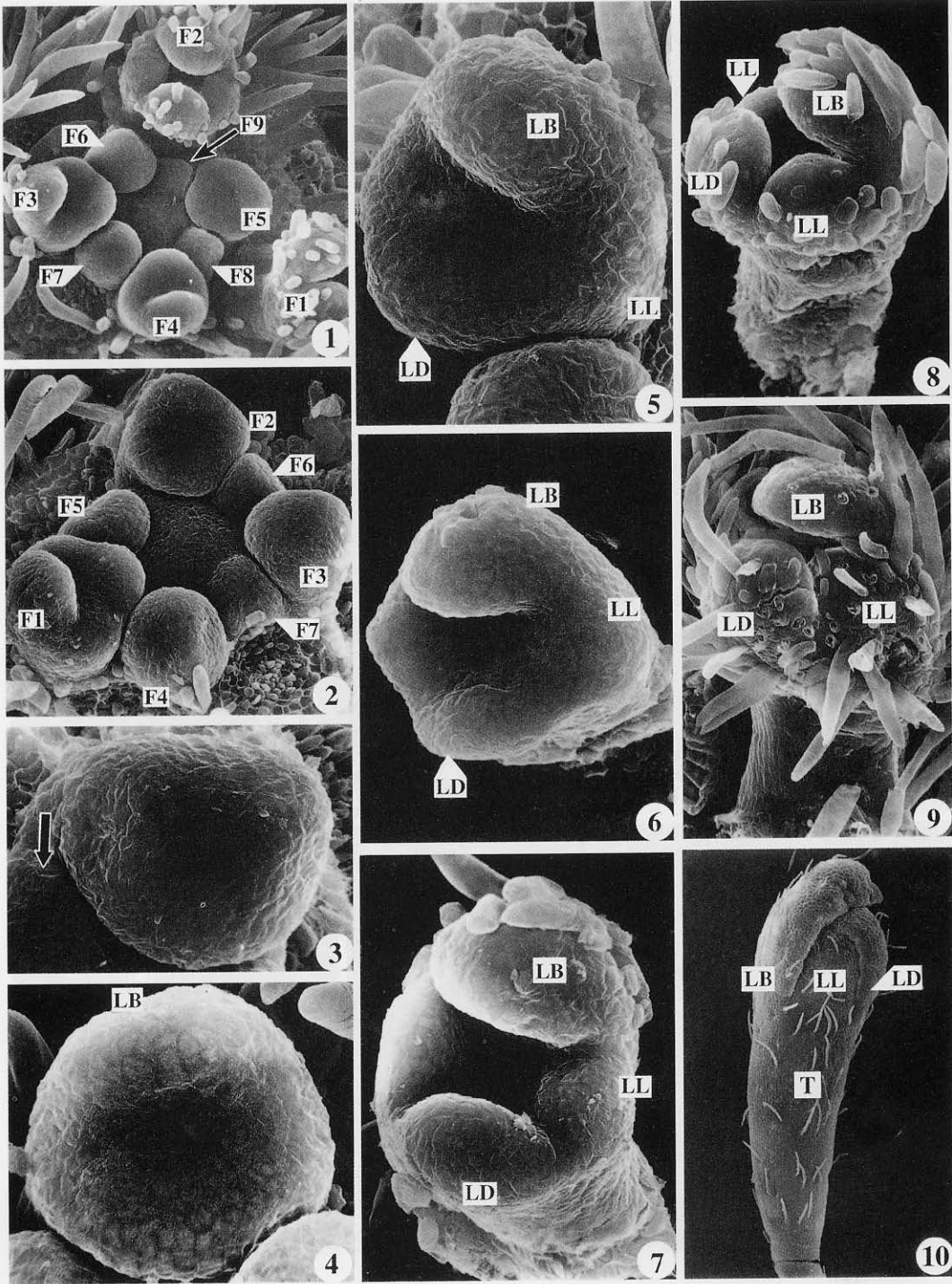
2.4 Disc initiation and development

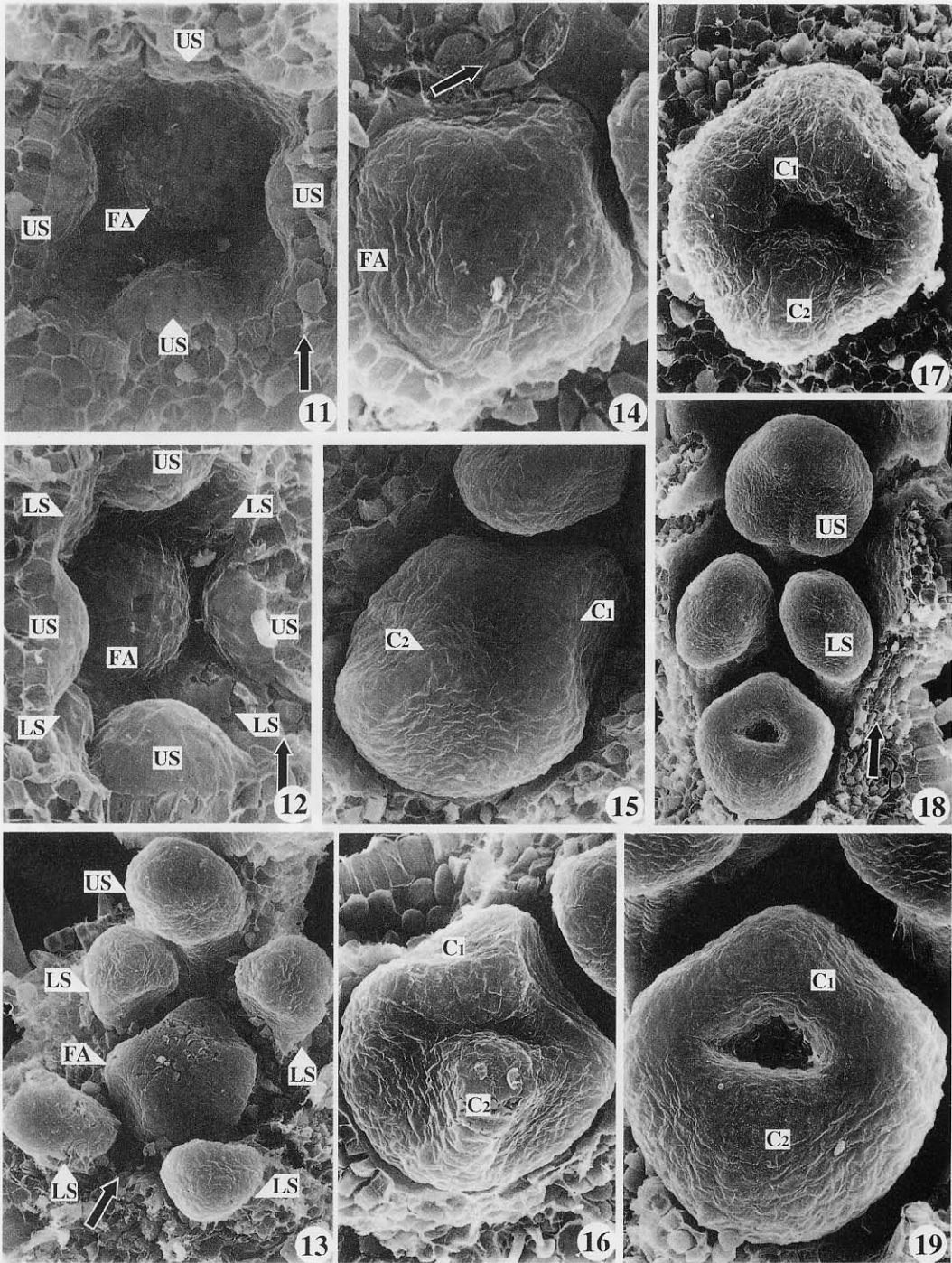
When the stamens in the lower whorl were about 266 μm high, a semi-annular disc was initiated at the abaxial base of the floral tube (Figs. 27, 28). The disc primordium was less active at base of the two filaments of the lower whorl than in other region, which led to a gap at the base of the filament respectively. The gaps divided the disc into a middle part and two lateral parts, and the former was slightly higher than the latter at early stage (Figs. 28, 29). As growing upward, the middle part and two lateral parts were connected from the base of gaps upward (Figs. 30 ~ 32). Sometimes one lateral part grew faster than the middle part (Fig. 32). However, the disc remained deep or shallow dents at the position next to the filaments of the lower whorl (Figs. 33 ~ 35). There were three depressed lines in the back surface of the disc next to the filaments (Fig. 34). At anthesis, the length of a scale-like disc was about 767 μm high, one third of the pistil in height (Fig. 35).

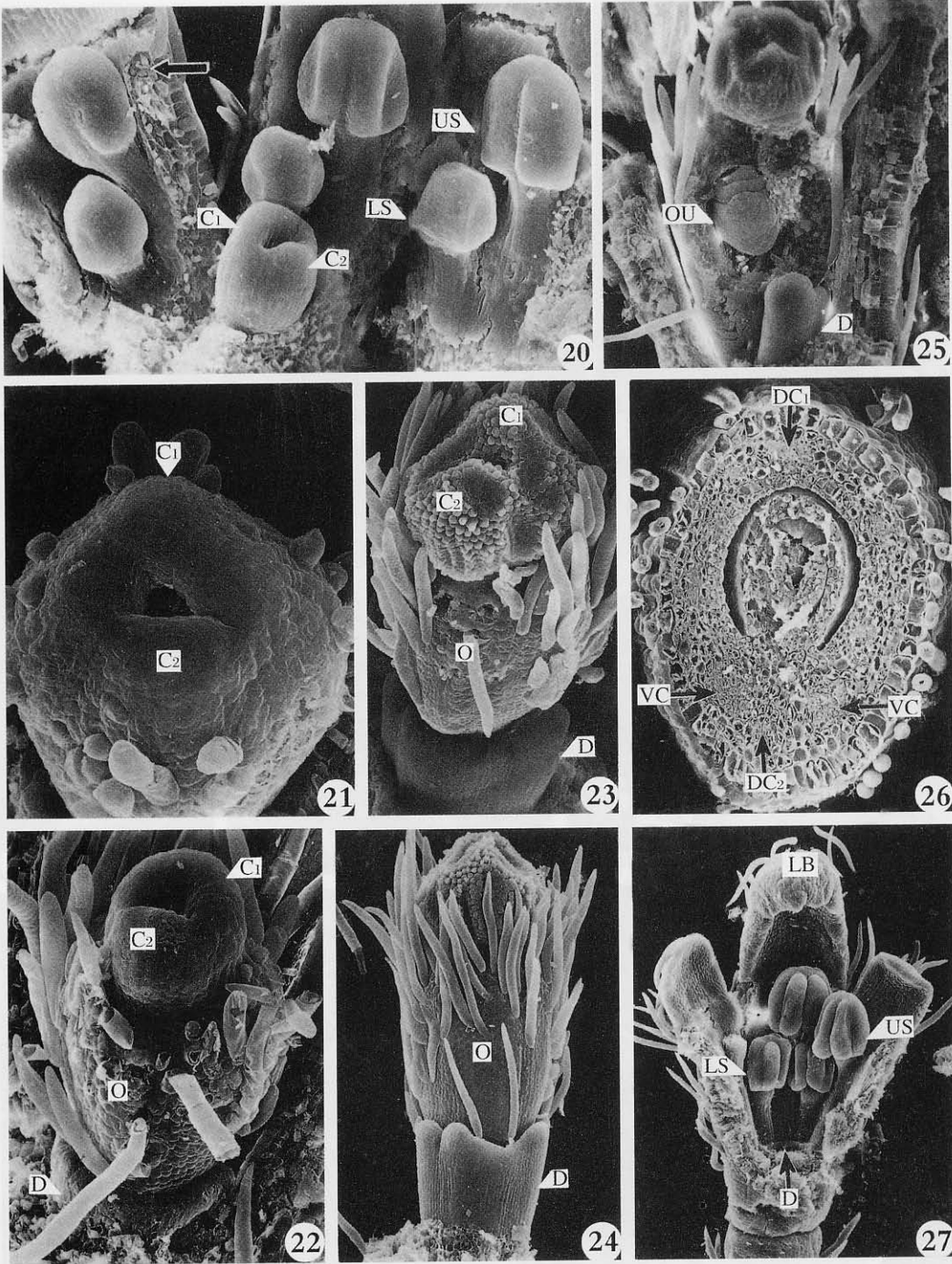
3 Discussion

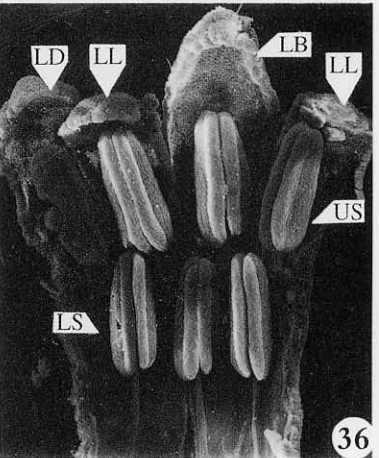
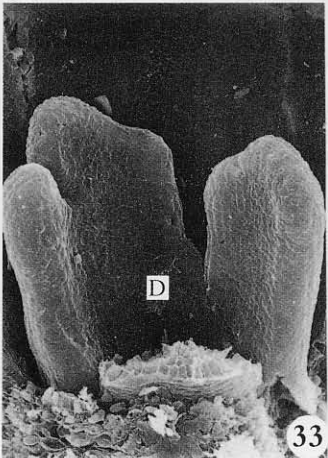
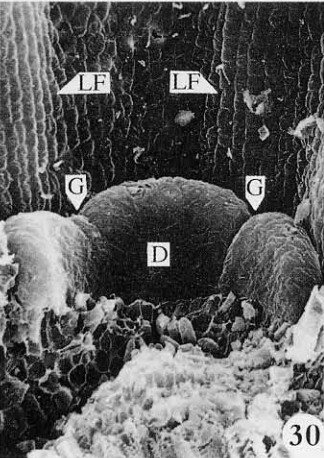
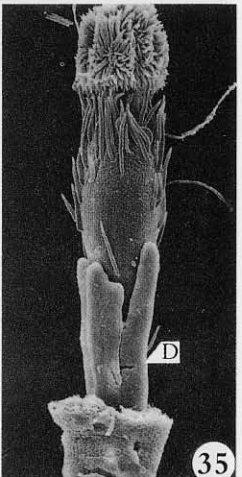
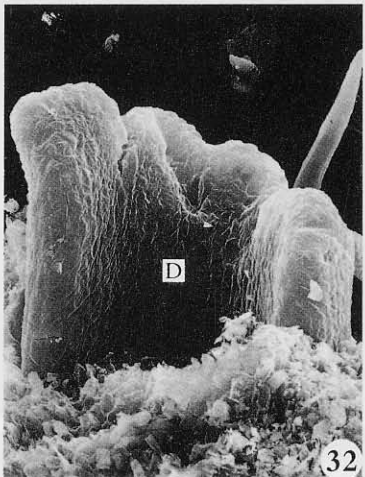
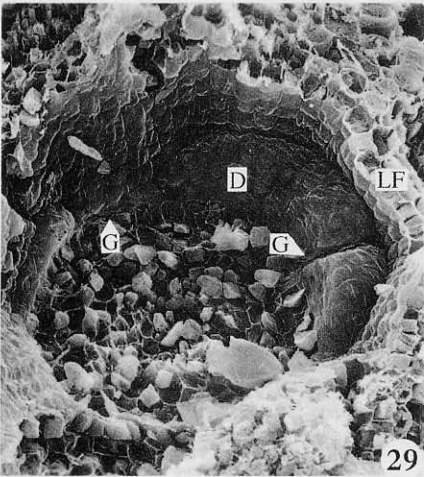
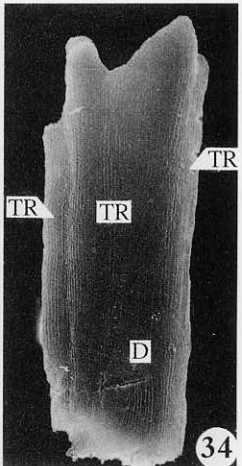
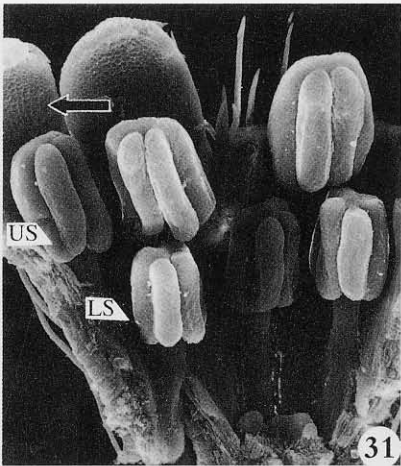
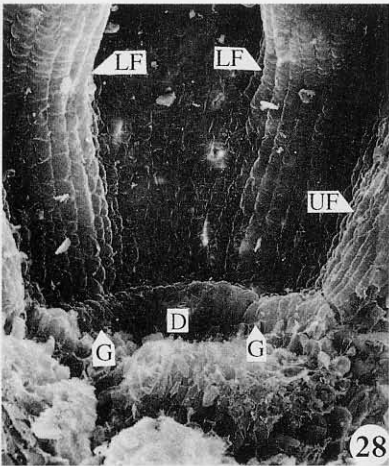
3.1 The floral symmetry

According to Tucker (1984), the shape of the floral apex before organ initiation is correlated with the symmetry at later stages in many plants. This seems to be true in the floral development of *W. delavayi*. The primary floral primordium in *W. delavayi* was obliquely cone-shaped with a gradual slope from the narrow adaxial bottom to the wide abaxial top, rather than circular-shaped. Correlatively, the initiation of floral organs followed a unidirectional or modified unidirectional sequence, in which the floral organs at the abaxial side were always initiated earlier than others in the same whorl. The difference in the floral organs of the same whorl became more manifested during development. The zygomorphy was established before the initiation of the floral organs and further pronounced in the early and middle developmental stages. However, it deserved special attention that the floral organs in the same whorl were almost actinomorphic at anthesis. Apparently, there









Abbreviation: C1. Adaxial carpel; C2. Abaxial carpel; LD. Adaxial floral lobe; LB. Abaxial floral lobe; LL. Lateral floral lobes; D. Disc; DC1. Dorsal bundles of the fertile carpel; DC2. Dorsal bundles of the sterile carpel; F. Floral primordium; G. Gap; FA. Floral apex; LF. Filament of lower whorl stamen; LS. Lower whorl stamen; O. Ovary; OU. Ovule; T. Floral tube; TR. Trace on the back of disc; UF. Filament of upper whorl stamen; US. Upper whorl stamen; VC. Ventral carpellary bundles.

Figs. 1 ~ 10 Initiation order of the floral primordium, and initiation and development of the floral lobe and tube. 1 ~ 2. Top view of the young inflorescence, showing initiation order and the shape of the floral primordium. 1. Initiation of floral primordia in anticlockwise order by apex of the inflorescence, note the youngest floral primordium (F9) with a gradual slope from the narrow adaxial bottom to the wide abaxial top ($\times 132$). 2. Initiation of the floral primordia in clockwise order by apex of the inflorescence, note the youngest floral primordium (F7) with a gradual slope from the narrow adaxial bottom to the wide abaxial top ($\times 180$). 3. The ellipsoidal floral primordium (Arrowhead shows direction from the abaxial side to the adaxial one) ($\times 480$). 4 ~ 10. Initiation and development of the floral lobe and tube. 4. Initiation of the abaxial floral lobe primordium ($\times 480$). 5. Initiation of adaxial and lateral floral lobes primordia ($\times 480$). 6. Oblique-top view, showing sub-equal floral lobes primordia at the adaxial and lateral sides ($\times 360$). 7 ~ 8. Development of floral lobes, showing that the adaxial one exceeds the lateral ones. 7. Top view of the flower ($\times 360$). 8. Lateral view of the flower at the stage slightly later than the one in Fig. 7 ($\times 240$); 9 ~ 10. Imbricate aestivation of floral lobes. 9. Oblique-lateral view of the flower, showing that the adaxial floral lobe overlaps two lateral ones ($\times 180$). 10. Lateral view of the flower, showing the adaxially bent floral tube and the imbricate aestivation in which the adaxial lobe overlaps the lateral ones, and the three adaxial and lateral ones are overlapped by the abaxial one ($\times 21$).

Figs. 11 ~ 19 Initiation and development of the androecium and the gynoecium. 11 ~ 12. Unidirectional initiation of stamens primordia and dome-shape floral apex (Arrowhead shows direction from the abaxial side to the adaxial one). 11. Top view, showing initiation of the upper whorl stamens ($\times 600$). 12. Oblique-top view, showing initiation of the lower whorl stamens alternating with the upper whorl ones ($\times 600$). 13. Top view, showing stamens and the floral apex (The upper whorl stamens at the abaxial and lateral sides were removed, and arrowhead shows direction from the abaxial side to the adaxial one), note the differentiation of anther and filament in the upper whorl adaxial stamen, and a change of the shape of the floral apex from dome-shape into tetragonal form leaned by four lower whorl stamens primordia ($\times 300$). 14. The tetragonal floral apex (Arrowhead shows direction from the abaxial side to adaxial one) ($\times 768$). 15. Top view of the carpels primordia, note that two carpels primordia are initiated from the abaxial and adaxial region elevating from the floral apex, in which the abaxial side is higher than the adaxial one ($\times 480$). 16. Oblique-top view of two carpel primordia, showing a slope from the dorsal summit to ventral region in each one ($\times 480$). 17. Top view of two young carpel, note fusion at the lower part of the two carpels, and adaxial carpel infolding toward the abaxial side because of faster lateral growth ($\times 480$). 18. The adaxial stamens and gynoecium (Arrowhead shows direction from the abaxial side to the adaxial one, and the abaxial and lateral stamens in upper whorl and the two abaxial stamens in lower whorl were removed), note that median furrow appears in the upper whorl adaxial stamen, when the lower adaxial stamens differentiates into anther and filament ($\times 180$). 19. Top view of magnified gynoecium from Fig. 18, showing further infolding adaxial carpel ($\times 420$).

Figs. 20 ~ 27 Development of the androecium and the gynoecium, and initiation of the disc. 20. Lateral view of stamens and gynoecium (The stamens on one side of laterals were removed, and arrowhead shows direction from the abaxial side to the adaxial one), showing that in upper whorl stamens transverse furrows become visible in the larger abaxial and lateral stamens, while median furrow can be seen only in the smaller adaxial stamen, and the lower whorl stamens are equal in size but smaller than the upper whorl ones. Note that lateral growth of the abaxial carpel is far slower than that of adaxial one ($\times 132$). 21 ~ 23. Development of the stigma, note that abaxial and adaxial carpels could be still seen from top view of the stigma. 21. Oblique-top view of gynoecium, showing the forming stigma ($\times 360$). 22. Oblique-lateral view, showing early development of stigma and disc. Note disc at abaxial side ($\times 180$). 23. Top view of gynoecium at late stage, showing papillae on the stigma. Note disc at abaxial side ($\times 120$). 24. Lateral view of gynoecium and disc at late stage, note disc at abaxial side ($\times 78$). 25. Longitudinal sectional view, showing bitegminous ovule ($\times 90$). 26. The transverse section of the mature ovary, showing that two ventral carpellary bundles laterally locate nearer the dorsal carpellary bundles of the sterile carpel ($\times 120$). 27. Lateral view of flower (the gynoecium, the adaxial and lateral stamens in upper whorl and the two adaxial stamens in lower whorl were removed), showing relative time of initiation of disc. Note that disc just initiated at abaxial side when lower whorl stamens had developed up to a stage that four clear anther cells became visible ($\times 60$).

Figs. 28 ~ 36 Initiation and development of disc and androecium. 28 ~ 29. Initiation of the disc primordium. 28. Magnified disc primordium from Fig. 27, showing that disc primordium is initiated from the abaxial base of floral tube. Note gap at base of lower whorl abaxial filaments ($\times 300$). 29. Early development of the disc primordium, showing gaps between the higher middle part and the lateral parts ($\times 360$). 30, 32 ~ 33. Lateral view of the ventral side of the disc at different developmental stage, showing that the shape of the disc top changed in the following development. 30. Fusion of disc at the base, note gaps between the higher middle part and the lateral parts ($\times 300$). 31. Lateral view at stage similar to that in Fig. 30, showing relation between disc and stamens (one stamen of laterals in upper whorl and one adaxial stamen in lower whorl were removed, and arrowhead shows direction from the abaxial side to the adaxial one). Note that in upper whorl stamens the abaxial stamen is still larger than the adaxial one, and stamens in lower whorl are smaller than ones in upper whorl at this stage ($\times 66$). 32. One type of disc with one higher lateral part than middle part after early stage ($\times 240$). 33. Another type of disc with the middle higher part than two lateral parts after early stage ($\times 150$). 34. Lateral view of the dorsal side of disc at late stage. Note three traces leaned by the abaxial filaments ($\times 66$). 35. Lateral view of the abaxial side of the mature gynoecium with papillate hairs on the stigma, note that the disc is one third of the pistil in height. ($\times 30$). 36. Stamens just before anthesis (an adaxial stamen in lower whorl was removed), showing that all of the stamens are equal in size ($\times 18$).

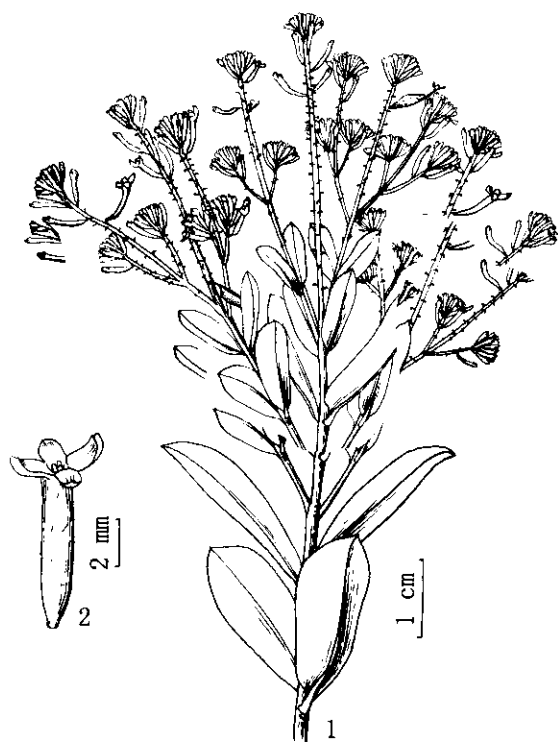


图 37 澜沧堇花 1. 花枝; 2. 花(李爱莉 绘)。

Fig. 37 *Wikstroemia delavayi* 1. Flower branch; 2. Flower.

(drawn by Li Ai-li)

should be a shift of growth pattern during the development of the floral organs. Stebbins (1950) suggested that the change of symmetry involved the development of unequal rates of growth, i. e. allometry, affecting either different directions of growth in the same organ or the relative growth of different organs. Ontogenetic process showed that the shift of the growth pattern occurred after early or at later developmental stage in different floral organs respectively. In the development of the gynoecium, the adaxial carpel exceeded the abaxial one in growth soon after primordial initiation and infolded toward the abaxial side. Finally, the adaxial carpel occupied the most part of the gynoecium. The four stamens in the lower whorl became almost equal in size at the early stage, whereas the four stamens in the upper whorl were different in size until the stage close to anthesis. The abaxial and adaxial floral lobes became almost equal in size at anthesis. However, the situation of the disc initiated only at the abaxial base of the floral tube was remarkably

different from that of other floral organs. Its remarkably zygomorphic character at initiation was maintained throughout the developmental process. It was obvious that the so-called actinomorphic flower in *W. delavayi* was subsequent to a secondary event, i. e. a shift of growth pattern, due to the unequal rates of the organ growth in the same whorl. This secondary radial symmetry might be related to pollination, which needs to be investigated further.

3.2 Nature and location of the disc and its correlation of the initiated sequence with other floral organs

Heining (1951) suggested that the floral tube of thymelaeaceous flower was appendicular in origin, and was composed of the fused based of the sepals and adherent stamen filaments, in which the disc was considered as a part of the androecium. In this study, the disc in *W. delavayi* was initiated at the abaxial base of the floral tube, and the initial gaps were located at the base of the filaments of the lower whorl stamens, and the disc lobes were basically alternate with the abaxial stamens of lower whorl. The development of the disc is strongly in favor of Heining's view (1951) that the disc should be interpreted as a part of the androecium rather than as a modification of the receptacle (Geber, 1889) and an independent structure (Skottsberg, 1972). The discs investigated in this species are all located at the abaxial side. The middle part of disc is always slightly higher than lateral parts in early development. All of these indicate that the initiation and development of the disc follow a similar pattern with that of other floral organs. In addition, the floral tube of all indi-

vidual flowers in *W. delavayi* bends toward the inflorescence axis at anthesis. Besides *W. delavayi*, further investigations show that the discs are all located at the abaxial side in species with scale-like or oblique disc in both *Wikstroemia* and *Daphne*. Correlatively, their mature floral tube always bend toward the inflorescence axis. These species include *D. holoserice* (Diels) Hamaya, *D. rosmarinifolia* Rehd., *D. modesta* Rehd., *D. gemmata* E. Pritz., *W. scytophylla* Diels, *W. dolicantha* Diels, *W. stenophylla* E. Pritz, etc. Whether the floral development of these species shares similar pattern with that of *W. delavayi* depends on further investigation. However, in other species with the annular or cup-shaped disc, such as *D. tangutica* E. Pritz., *D. longilobata* (Lecomte) Turrill, the floral tube is straight at anthesis. The morphology and location of the disc probably are correlated with the behaviour of the floral tube at anthesis. However, it is unknown whether these different situations are reflected in the development of the disc and related floral organs. Further investigation would be needed for the remained question.

3.3 The morphological nature of the gynoecium and its phylogenetic implication

The gynoecium with uniloculate ovary in *Wikstroemia* was frequently interpreted as possessing one carpel or two carpels by different authors (Gilg, 1894; Johnson, 1931; Eckardt, 1937; Heining, 1951; Lawrence, 1951). According to Heining (1951), one of two carpels in the syncarpous gynoecium degenerated to become sterile. This type of gynoecium was called as pseudomonomerous form by the authors who thought that it owns two carpels. In *Wikstroemia* Skottsberg (1972) observed a series of transition forms from the globose stigma, through slightly to deeply furrowed stigma to two separate stigmas, in which the division sometimes extended to the style. He considered the structural variation of the stigma as an indication of bicarpellary origin of the gynoecium. The development of gynoecium of *W. delavayi* showed that the abaxial carpel primordium was slightly higher than the adaxial one on the tetragonal floral apex at inception. Afterwards the abaxial carpel became suppressed in growth, and finally remained only at the median position of the abaxial side. This result indicates that the uniloculate ovary is in fact bicarpellate.

Among the genera with an uniloculate ovary, *Daphne* is most close to *Wikstroemia* in affinity. Although the gynoecia of both genera are uniloculate, the ventral carpellary vascular bundles locate at the position near the dorsal bundles of the abaxial carpel in *Wikstroemia*, whereas those in *Daphne* are at the position almost equi-distant from the dorsal bundles of two carpels (Heining, 1951). It needs further research to determine whether the difference in the relative position of the ventral carpellary bundles is involved in different origin of the uniloculate gynoecium. It might provide insight to the phylogeny and delimitation of the two genera.

Acknowledgments The authors are much indebted to Prof. Wang Wen-Tsai (Institute of Botany, CAS) for his valuable comments on this manuscript. We would like to express our gratitude to Prof. Gong Xun (Kunming Institute of Botany, CAS) for his help in the field. We are also grateful to Mr. Xiao Yin-Hou and Mr. Yang Xue-Jian (Institute of Botany, CAS) for technical assistance.

Reference

- Bentham G, Hooker J D, 1880. *Genera Plantarum*. London: L. Reeve & Co. 3: 186 ~ 201
- Crisci J V, Stuessy T F, 1980. Determining primitive character states for phylogenetic consideration. *Syst Bot*, 5: 112 ~ 135
- Domke W, 1932. Zur Kenntnis einiger Thymelaeaceen. *Notizbl Bot Gart Mus Berlin*, 11: 348 ~ 363
- Eckardt T, 1937. Untersuchungen über Morphologie, Entwicklungsgeschichte und Systematische Bedeutung des

- pseudomonomeren Gynoeceums. *Nova Acta Leopoldina*, 11. 5(26): 1 ~ 112
- Dute R R, Freeman J D, Henning F *et al.*, 1996. Intervascular pit membrane structure in *Daphne* and *Wikstroemia*——systematic implications. *IAWA J*, 17(2): 161 ~ 181
- Gerber M C, 1899. Les Passerina provençaux; essai de classification et recherches sur la nature du disque hypogyne et des saillies perianthiques. *Bull Soc Bot France*, 46: 108
- Gilg E, 1894. Thymelaeaceae. In: Engler A & Prantl K eds. *Die natürlichen Pflanzenfamilien*. Leipzig: Verlag von Wilhelm Engelmann. 3(6a): 216 ~ 245
- Halda J J, 1999. Some taxonomic problems in the genus *Daphne* L. II. *Acta Mus Richnov (Sect Natur)*, 6(3): 195 ~ 233
- Hamaya T, 1959. Dendrological studies of the Japanese and some foreign genera of the Thymelaeaceae. *Bull Tokyo Univ Forests*, 55: 1 ~ 80
- Hamaya T, 1963. Taxonomical notes on Daphneae (Thymelaeaceae). *Acta Horti Gothob*, 26: 64 ~ 99
- Heining K, 1951. Studies in the floral morphology of the Thymelaeaceae. *Amer Journ Bot*, 38: 113 ~ 132
- Hou D, 1960. Thymelaeaceae. In: van Steenis C G G ed. *Flora Malesiana*. Leyden: Noordhoff International Publishing. Ser I. 6 (1): 1 ~ 48
- Hutchinson J, 1967. *The Genera of Flowering Plants*. Oxford: Clarendon Press. 246 ~ 260
- Huang S C, Zhang C Y, 1999. Thymelaeaceae. In: Wu C Y ed. *Flora Reipublicae Popularis Sinicae*. Beijing: Science Press. 52 (1): 292 ~ 385
- Johnson A M, 1931. *Taxonomy of the Flowering Plants*. New York: The Century Co. 411
- Lawrence G H M, 1951. *Taxonomy of Vascular Plants*. New York: The Macmillan Company. 625
- Lecomte H, 1914. *Notulae Systematicae T. III*. Paris: Herbarium du Museum de Paris. 128 ~ 131
- Meisner C F, 1857. Thymelaeaceae. In: De Candolle A, *Prodromus syst nat regni veg Parisiis*. 14: 493 ~ 605
- Nakai T, 1928. Daphnaceae. In: *Flora Sylvatica Koreana*. 17: 31 ~ 45
- Skottsberg C, 1972. The Genus *Wikstroemia* Endl. in the Hawaiian Islands. Göteborg: Kungl. Vetenskaps-och Vitterhets-Samhället. 9 ~ 21
- Stebbins G L, 1950. *Variation and Evolution in Plants*. New York: Columbia University Press. 485
- Tan K, 1980. Study in the Thymelaeaceae II: a revision of the genus *Thymelaea*. *Notes R B G Edinb*, 38(2): 189 ~ 246
- Tucker S C, 1984. Origin of symmetry in flowers. In: White R A, Dickis W C eds. *Contemporary Problems in Plant Anatomy*. New York: Academic Press. 351 ~ 359

摘要 通过扫描电镜对澜沧蕤花 *Wikstroemia delavayi* 花部的形态发生过程进行了观察和分析,旨在为该属的系统学研究提供花部发育形态学资料。澜沧蕤花花部的发生和早期发育呈远轴面向近轴面的顺序,但这一式样由于近轴面的器官在早期发育之后生长加速发生了转变。因此,花开放时所表现的所谓辐射对称,显然是由同一轮器官的异率生长所导致的次生现象。花盘发生于花萼筒基部的远轴面上,与花萼、雄蕊的发生间隔时间较长。花盘原基在下轮雄蕊着生处凹陷或间断,与之相对应,花盘裂片与下轮雄蕊呈互生。由此,花盘显然不是花托的一部分,也不是象花萼、雄蕊和心皮一样的独立结构,将其解释为雄蕊群的一部分更合理。花盘的发生和早期发育及其着生位置同其他花部器官的发生和发育式样具有明显的相关性,这种相关性对进一步阐明瑞香属 *Daphne* 和蕤花属 *Wikstroemia* 的系统发育关系具有一定意义。根据对雌蕊群的发生和发育过程观察,该种的子房是由一个近轴面的可育心皮和一个远轴面的不育心皮融合而成的单室子房,为假单心皮雌蕊。尽管蕤花属和瑞香属均属于单室子房,但澜沧蕤花的子房维管束中的腹束排列于中轴位置,而目前资料显示瑞香属植物的腹束接近于侧膜位置,这方面仍需进一步研究。

关键词 花部形态发生; 两侧对称性; 花盘; 假单心皮雌蕊; 澜沧蕤花; 瑞香科